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By

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IDENTIFICATION OF GEOGRAPHIC FORMS OF COMMON DOLPHINS
(Delphinus delphis) FROM AERIAL PHOTOGRAPHS

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Abstract

At least four morphologically distinct forms of common dolphins are found in the eastern Pacific. We compared length data for common dolphins photographed from the northern, central and southern regions as defined by Perrin et al. (1985) and found significant differences in average length for adult animals (>150 cm) and for "adult females" defined for our purposes as animals accompanied by calves. Analyses of calculated birth dates for calves demonstrated differences in timing of reproduction between the geographically adjacent forms. Length distributions from aerial photographs and samples collected from the purse seine fishery were strikingly similar providing mutual support for the validity of each. This work demonstrates a new, noninvasive method for obtaining unbiased life history and morphological data.

Introduction

The common dolphin, Delphinus delphis, is a polymorphic species with a cosmopolitan distribution in subtropical and temperate waters. Evans (1975; 1982) examined the morphology and distribution of this species in the eastern Pacific and described five distinct forms: 1) a short-beaked form off southern

California; 2) a short-beaked form off Baja California; 3) a large, long-beaked neritic form north of 20° N; 4) a short-beaked central tropical form; 5) and a southern short-beaked form. He also suggested the possibility of an "equatorial-oceanic" population. Based on more sightings and a larger sample of aged specimens, Perrin et al. (1985) combined the southern California and Baja short-beaked populations and expanded the range of the southern form to include Evan's equatorial-oceanic group (Figure 1). They defined a southern stock based on a hiatus of sightings between the central and southern populations.

Most specimens used in the reports cited above were killed incidental to purse seine fishing for yellowfin tuna (Perrin 1969). The use of fishery samples to obtain data on life history and morphology usually raises questions concerning potential bias in the sample (e.g., Perrin and Reilly 1984). For example, the vulnerability of dolphins to fishing mortality may vary with age, sex or reproductive condition. If so, then samples obtained from the fishery are biased, and the validity of studies using these samples are in question. In addition, the geographic distribution of specimens collected from the fishery is restricted to areas where common dolphin and tuna associate.

In this report, we examined the geographic forms of common dolphins from an entirely different data source. We compared length distributions of common dolphins measured on aerial photographs taken over schools from the northern, central and southern regions (Figure 1). We also compared lengths of adult animals swimming with calves, defined as "adult females," between these regions and examined calculated birth dates of calves for evidence of reproductive seasonality. Similar techniques have been applied to the study of large cetaceans (Scott and Winn 1980; Whitehead and Payne 1976; Cubbage and Calambokidis 1987; Sumich 1984; 1986; Sumich and Show 1992; Koski et al. 1992; Withrow and

Angliss 1992), but this is the only large scale application of aerial photogrammetric sampling to the study of geographic concordance of intraspecific differences in small cetaceans (Scott and Perryman 1991).

Methods

Photographic Sampling

Aerial photographs of 14 schools of common dolphins were used for this report (Table 1). We took the photographs from a Hughes 500D helicopter that was deployed onboard the NOAA Ship David Starr Jordan. This sampling was part of a research program fielded by the National Marine Fisheries Service to monitor trends in abundance of dolphin stocks that are killed incidental to purse seine fishing for yellowfin tuna (Holt and Sexton 1989).

The photographs were taken with a KA45A military reconnaissance camera that was mounted vertically below the fuselage of the helicopter. The camera was designed to collect high resolution, medium format (127 mm) images from high speed aircraft flying at low altitudes. It has a medium focal length, fixed focus lens (152 mm) with a maximum aperture of f2.8. The camera's focal plane shutter consists of two metal curtains that sweep a slit of light along the film plane, parallel to the direction of flight. When used from a moving platform, this type of shutter can cause some distortion and blurring of the image due to the relative movement between the camera and the scene. The KA45A counteracts this problem with a forward image motion compensation (FMC) system that moves the film at precisely the same speed and direction as the image while the shutter is open. The speed of film movement is a function of altitude and ground speed. FMC reduces distortion and greatly improves image resolution.

All of the photographs were taken with Kodak Aerial Plus-X black and white film. We exposed the film through a medium yellow filter (Wratten #9) to reduce the amount of blue light reaching the film, thus enhancing the contrast between the dolphins and their

blue background. The photographs were taken at altitudes between 200 and 300 meters and at a ground speed of about 113 km/hr. As each frame was exposed, a computer-based data acquisition system automatically logged both the altitude and time. This system also allowed the scientists in the helicopter to record other information for each photo-pass over the school.

Length Determination

We selected dolphins for measurement that were swimming parallel to and very near the surface. Dolphins that were jumping, surfacing, or diving were excluded from the sample. We measured the dolphins from the tip of the rostrum to the trailing edge of the tail flukes (Figure 2). We selected these points because the fluke notch was very difficult to see in most of the images. For adult specimens, this measurement is about 2.5 cm longer than standard length (Norris 1961; Heyning and Perrin 1991).

We measured the dolphins on the original negatives with the aid of a stereocomparator, which records distance measurements to the nearest micron. A micron corresponds to roughly 1.5 cm on the ground from our normal sampling altitude of 230 m. These measurements were supplemented and verified with a variable ocular micrometer installed in a stereo zoom microscope.

In vertical photographs, the relationship between the size of an object and its image on the film is determined by the ratio of the focal length of the lens and the distance from the camera to the object. This ratio is commonly called the scale of the photograph and is defined as

$$\text{scale} = A/f = o/i$$

where

A = altitude

f = lens focal length

o = size of object photographed, and

i = size of the image of the photographed object.

In our study, focal length remained constant and the scale of each image was determined by the altitude recorded from the radar altimeter. To calibrate the radar altimeter, we photographed objects of known size (target arrays ashore and the ship at sea) and compared altitude derived from measurements with recorded altitude.

Measurement Precision and Accuracy

There are several potential sources of error in determining the true size of an object from its image on an aerial photograph. In topographical aerial photogrammetry, objects of known size and configuration can be photographed and then measured to determine accuracy of a photographic sampling system. When aerial photogrammetry is applied to the study of marine mammals, known sized animals are generally unavailable and indirect techniques must be used to estimate the magnitude of the errors inherent in the sampling. In this study, we conducted three experiments to examine the accuracy and precision of our data.

To test the accuracy of our measurements, we photographed three painted dolphin targets from altitudes of 200, 240, and 260 meters, the range of altitudes we use in the field. We painted the dolphins light blue/grey against a darker blue background to simulate the low subject to background contrast we encountered over the tropical Pacific. Measurements of known sized objects near the targets were used to determine the scale of each image. For each pass, the three dolphins were independently measured ten times in sequence by two individuals.

Because measuring targets was probably easier than measuring dolphins swimming under water, we also tested the precision of our length measurements by repeatedly measuring five dolphins from a single photograph. We selected dolphin images of varying quality and of both adults and calves. The test was performed rapidly and at the end of eight hours of measurement in

an attempt to add the element of fatigue to the sample.

In addition to errors in measurement of the images, errors in instantaneous readings of altitude, image distortion from tip or tilt of the camera, and the refraction of light as it passes through the water all impact the accuracy of our dolphin length measurements. Also, the flex of the bodies of the dolphins associated with normal swimming movements changes their apparent length when viewed from above. Dolphins that were moderately arched or tilted were easily eliminated from the data set because their rostrums or flukes were not visible from above. However, measurements of animals that were slightly arched or tilted still remain in the data set and estimates of the true length of these dolphins are probably negatively biased.

To determine the variability in the measurements associated with all these sources of error, we examined the data for dolphins that were measured in three or four photographs from the same pass. In this exercise and the two described above, we used the coefficient of variation as a measure of the relative precision of the measurements.

Data Analysis

Our photographs included schools from each of the three management units recommended by Perrin et al. (1985; Figure 1). In the northern region, a short-beaked and a much larger long-beaked form occur sympatrically but apparently do not school together (Evans 1975). We examined the length distributions of the schools from this region first to determine the stock mix in this sample. Only data for the short-beaked form were used in comparisons between the three regions.

In Perrin et al. (1985) morphological differences between putative stocks of common dolphins were demonstrated by comparing the means of length distributions for mature male and female specimens from the northern and central regions. Obviously, we could not directly examine the sexual characters of the dolphins in

our photographs, so we devised two methods for stratifying our length samples for comparison with the strata used by Perrin and his co-workers. These two methods and a technique for detecting reproductive seasonality are described below.

Method #1 - Modes

Our length distributions from each region included a small sample of calves and young animals and a larger sample mode containing subadult and adult age classes (Figure 3). We eliminated the youngest animals from the samples using length as the limiting criteria (< 150 cm) and tested for regional differences in size with an ANOVA. We selected the Tukey-Kramer procedure for pair-wise comparisons because of its power in tests with unequal sample sizes (Day and Quinn 1989). Because the selection of 150 cm as a minimum size for this sample was somewhat arbitrary, we repeated the analysis with minimum values of 155, 160 and 165 cm.

Method #2 - "Adult Females"

The unique association between cows and calves has been noted for a wide range of cetaceans (Norris and Prescott 1961; Pryor and Kang 1980; Taber and Thomas 1982; Pryor and Shallenberger 1991; Wells 1991), and this behavior has been used to identify cows or adult females in several studies (Whitehead and Payne 1976; Würsig and Würsig 1980; Davis et al. 1983; Sumich 1984; Cubbage and Calambokidis 1987; Scott and Perryman 1991; Withrow and Angliss 1992). In our aerial photographs, calves (dolphins < 145 cm) were consistently found swimming closely alongside a larger animal (> 155 cm). The distance between these cow/calf pairs was about $1/4$ that between dolphins of approximately adult size. Based on the consistency of this association in all of our images and the work cited above, we have assumed that the larger animal swimming closely alongside a calf was an adult female. Because this determination was made entirely on behavior, we qualify the term with quotation marks, "adult female," whenever we are referring to a sample of lengths based on the above assumption. We conducted an

additional ANOVA as described above to test the hypothesis that "adult females" from the three regions did not differ in length.

Reproductive Seasonality

Typically, post-natal growth in delphinids is very rapid and almost linear for the first year. During this period when increases in length are large relative to the variability in length at age, seasonal modes in length distributions and frequency histograms of back projected birth dates have been used to investigate patterns of growth and reproductive seasonality for several stocks of tropical dolphins (Perrin et al. 1976; Perrin et al. 1977; Perrin and Henderson 1984; Barlow 1984; Hohn and Hammond 1985).

For common dolphins, only two unpublished documents were found that reported growth rates for specimens taken from the eastern Pacific (Hui 1973; 1977). In our first analysis of reproductive seasonality, we used estimates of average length at birth for the northern (81.3 cm) and central (79.0 cm) stocks (Hui 1977) and assumed that length at birth for the southern stock was the same as in the north. We used the estimated length at 1 year of 135 cm that Hui (1973) reported for common dolphins taken off southern California and Baja California, Mexico as our best estimate of the average length at 1 year for all three stocks. Assuming linear growth during the first year, we back-projected the birth dates for all dolphins less than 135 cm in length.

We generated a second distribution of back-projected birth dates using the published lengths at birth (80 cm) and 1 year (123 cm) for the northern spotted dolphin (Hohn and Hammond 1985). We selected the spotted dolphin as the model for this second data set because of its similarity in size to the common dolphin and the large body of published information on growth for this stock of tropical dolphins. Also, the growth rate from birth to one year we derived from the spotted dolphin length at age data is in closer agreement with more current information on first year growth rates for small cetaceans (Bright and Chivers 1991).

We used Kuiper's modification of Kolmogorov's test (modified K test) for comparisons of circular distributions (Batschelet 1965) to test the hypothesis that these birth date distributions were uniform (as done by Barlow 1984). This is a nonparametric test for goodness-of-fit for cumulative distributions. Because critical values for two-tailed tests have not been tabulated, this test was only applied in comparisons of sample distributions with uniform distributions.

All statistical tests not specifically referenced were performed with the program Super ANOVA distributed by Abacus Concepts, Inc., Berkeley, California. Tests were considered significant at $p < 0.05$ unless stated otherwise.

Results

Altitude Calibration

We compared calculated altitude (A_m) from measurements of known sized objects with simultaneous readings from our radar altimeter and found a consistent bias in the recorded altitudes (A_r). The linear regression equation shown below describes the relationship between the A_m and A_r .

$$A_m = 1.013A_r - 33.755 \quad (r^2 = .993)$$

For each school, this formula was used to correct the recorded altitude before the lengths of the dolphins were calculated.

During the 1990 field season, the radar altimeter failed and was returned to the manufacturer for repairs. When the instrument was reinstalled, we recalibrated it and found that the relationship between A_m and A_r had changed. The new relationship was

$$A_m = 1.016A_r - 12.211 \quad (r^2 = .992)$$

This relationship was used to correct the recorded altitude during the last two legs of the 1990 survey.

Accuracy and Precision in Length Determination

For half of the 18 samples, the measurements of the dolphin targets from the aerial photographs were within 1 cm of the true length of the painted dolphin figures (Table 2). The measurements from the lowest altitude were consistently smaller for all targets and interpreters, but the differences between lengths for this range of altitudes were too small to require corrections or a modification in sampling techniques.

Repeated measurements of targets or animals from a single photograph indicate that the errors associated with the measurement process are very small (Table 3). When we compared measurements for the same dolphin in three or four different frames, the mean and range for the coefficients of variation increased but still remained at an acceptably low level. The additional variability in this last sample probably results from scale errors (imprecision in altimetry, camera tip or tilt, and refraction), which can introduce either a negative or positive bias, and the change in apparent length associated with swimming movements which should result in an underestimate of true length.

Length Distribution Comparisons

Four of the five schools from the northern region were found in the shallow, near-shore habitat occupied by both the short-beaked and the larger (~28 cm for adult females; Heyning and Perrin 1991) neritic or long-beaked forms of common dolphin (Table 4). When we compared the average lengths of dolphins >150 cm and of "adult females" for the five schools from the northern region, it was obvious that the animals in one of the schools were much larger on average (about 25 cm) than those from any of the other schools. Based on this size difference and the agreement of our data on this school with published lengths for specimens from the long-beaked form of common dolphins (Heyning and Perrin 1991), we identified

this school as neritic or long-beaked common dolphins and did not use these lengths in any of the regional comparisons that follow.

We conducted an ANOVA to test the hypothesis that the length samples (Figure 4) for dolphins > 150 cm from the three regions did not differ and the hypothesis was rejected ($p < 0.01$). The Tukey-Kramer post hoc tests found that all three regions differed significantly from one another when the minimum lengths for the samples were 150, 155 and 160 cm (Table 5). At 165 cm, the northern and southern regions no longer differed significantly, but they both differed from the central region at the $p < 0.01$ level.

When we repeated the analysis using only data for "adult females" (Figure 5) from each region, we found significant differences ($p < 0.01$) between the central sample and the northern and southern samples. The northern and southern samples differed at the 0.05 level (Table 5).

Birth Date Distributions

Our analysis of the distribution of the back-projected birth dates revealed three distinct patterns of reproductive seasonality (Figure 6). In the northern region, most births occurred in the first six months of the year although some calving occurred throughout the year. This pattern was found to differ significantly ($p < 0.01$) when compared (modified K test) with a projected uniform distribution (Figure 7). In the central region, the back-projected birth dates were distributed throughout the year, and the modified K test revealed no significant difference between the sample and a uniform pattern of births ($p > 0.10$; Figure 8). The sample from the southern region showed the strongest seasonality, with all calving occurring during the first 6 months of the year. This distribution differed significantly from the uniform ($p < 0.01$; Figure 9). When we repeated these analyses using birth date distributions generated from the published average size at birth and at one year for spotted dolphins (Hohn and Hammond 1985) to determine the rate of growth, the peaks in reproduction shifted in timing but the relative

patterns and test results remained the same (Figure 10).

Discussion

The accuracy of the target measurements (average error < 1%) and the precision of repeated measures from a single image (CVs average ≈ 0.01) reported here are very similar to those documented in several other aerial photographic field studies (Croze 1972; Scott and Winn 1980; Davis et al. 1983; Cabbage and Calambokidis 1987; Nerini et al. 1987; Koski et al. 1992). We also compared the lengths of dolphins measured from three or more successive frames to estimate the amount of variability in length determination resulting from errors in altitude measurement and the flex of the dolphins. As we expected, these measurements were more variable and the average of the coefficients of variation increased to 0.026. These data are comparable with average CVs of 0.016 and 0.024 for repeated photographs of bowhead whales (Nerini et al. 1987; Koski et al. 1992) and of 0.014 for repeated photographs of gray whales (Sumich 1984).

There are two known sources of bias in the length data that we presented in this paper. We measured to the trailing edge of the fluke rather than to the base of the fluke notch, which introduced a positive bias of about 2.5 cm for adult dolphins. Also, for an unknown proportion of the dolphins that we measured, the flex of their bodies and their orientation relative to the water's surface caused us to underestimate their length. Based on the striking similarity between our length sample for "adult females" and the published length data for adult females (Perrin et al. 1985; Heyning and Perrin 1991), the positive and negative biases associated with our sampling technique appear to be about equal (Table 6).

We calculated the birth dates of dolphins approximately ≤ 1 year old to see if there was any evidence for differences in reproductive seasonality, which could provide a barrier to gene flow between adjacent putative stocks. By this effort, we are not

trying to imply that we can accurately determine the age of a young dolphin from a length measurement. Rather, we feel that by applying the same technique to geographically isolated groups of dolphins we can detect differences in patterns of reproduction.

In the more temperate environments to the north and south, we found a pulse in reproduction from January through July. Reproductive seasonality was strongest in the southern stock, which inhabit the region that displays the widest range of oceanographic parameters of the three (Au and Perryman 1985; Reilly and Fiedler 1990). In the more typically tropical surface waters, which provide the habitat for the central stock, reproduction was distributed evenly throughout the year. This pattern of strong reproductive seasonality in the southern habitat in contrast to the more even distribution of births in the tropical waters to the north is similar to that demonstrated for spotted dolphins (Barlow 1984).

The data that we have reported here support the recommendations by Perrin et al. (1985) that common dolphins sighted within 100 nm of the Pacific coast of Baja must be identified to stock based on size, beak length and color pattern rather than by location. Based on differences in length between the northern and central putative stocks and a hiatus in distribution between the southern and central stocks, the same authors recommended that the northern, central and southern populations of short-beaked common dolphin should be managed as separate units. We have strengthened that argument by demonstrating differences in morphology between the southern and central regions and detecting differences in reproductive seasonality between all adjacent regions. However, although our sample shows a clear difference in morphology and timing of reproduction between the common dolphins from the central and southern regions, the data for the southern stock were drawn from only two schools that were found at the eastern edge of the distribution for this geographic form. More sampling of the southern form is needed to determine whether these data are representative of the entire southern region.

The results of our initial application of this length sampling system are very encouraging. We have developed a technique for collecting information on morphology and life history of small pelagic cetaceans that is independent of fishery-induced mortalities. This provides us with a tool for examining potential biases in our existing life history data base and the ability to sample in areas or seasons that the fishery is not active.

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Table 1. Schools of common dolphins used in length comparison study.
School size determined by observer estimates or counts from photographs.

Flight Date	School Position	Estimated School Size	Number Measured
9/14/88	00° 41'N; 109° 59'W	1 5 5	10
9/17/88	00° 02'N; 104° 25'W	1 8 4 0	40
10/10/88	07° 05'N; 089° 08'W	8 7 0	25
10/16/88	08° 49'N; 092° 08'W	6 4 9	57
12/1/88	23° 25'N; 112° 19'W	3 4 3	72
10/19/89	07° 56'N; 091° 55'W	2 2 6	68
10/19/89	07° 54'N; 092° 02'W	1 6 7	57
11/15/89	07° 04'N; 094° 16'W	3 0	9
11/15/89	07° 03'N; 094° 16'W	3 7 7	37
10/15/90	09° 35'N; 089° 36'W	1 2 5	85
12/5/90	30° 10'N; 116° 16'W	5 6 2	171
12/5/90	30° 16'N; 116° 12'W	1 1 7 5	393
12/5/90	30° 31'N; 116° 15'W	6 0 0	43
12/5/90	30° 47'N; 116° 22'W	1 1 0 0	274

Table 2. Lengths for three painted dolphin targets measured independently by two individuals. Each length is the mean of 10 measurements. True target length in parentheses.

Altitude (m)	Dolphin Target # 1 (84.6 cm)		Dolphin Target # 2 (177.4 cm)		Dolphin target # 3 (191.5 cm)	
	# 1	# 2	# 1	# 2	# 1	# 2
200	84.9	84.4	175.7	174.3	190.7	191.3
240	85.1	86.1	176.6	178.7	191.1	192.1
260	86.3	85.7	176.3	178.0	192.8	192.8

Table 3. Measurement precision, expressed as coefficients of variation, for replicate measurements of dolphin-shaped targets and of dolphins from single frames, and for measurements of dolphins from 3-4 successive frames.

Measured Object	# Dolphins Measured	Measurements per Dolphin	Mean of CVs	Range of CVs
Dolphin Targets Individual #1	3	30	0.008	0.005-0.012
Dolphin Targets Individual #2	3	30	0.014	0.007-0.020
Dolphins in one frame	5	5	0.009	0.004-0.012
Dolphins in different frames	54	3 - 4	0.026	0.001-0.083

Table 4. Depth, distance to shore, and size data for common dolphin schools photographed off of Baja California.

School #	Distance to Shore (km)	Depth (m)	Mean Length (>150 cm)	Mean Length (cm) "Adult Females"
1	19	164	205.6	206.2
2	27	182	180.6	182.3
3	19	155	181.3	179.1
4	16	150	177.8	180.3
5	103	3300	168.8	172.8

Table 5. Summary of mean lengths and results of Tukey-Kramer pairwise tests for the northern (Nor), central (Cen) and southern (So) regions.

Subsample Criteria	Mean Length Comparisons		
	Nor/Cen (cm)	Cen/So (cm)	Nor/So (cm)
> 150 cm	179.0/191.9**	191.9/183.8**	179.0/183.8*
> 155 cm	179.6/192.4**	192.4/183.8**	179.6/183.8*
> 160 cm	180.7/193.1**	193.1/184.8**	180.7/184.8*
> 165 cm	182.0/193.3**	193.3/185.7**	182.0/185.7
"adult females"	179.2/194.8**	194.8/184.3**	179.2/184.3*

* = $p < .05$

** = $p < .01$

Table 6. Comparison of published length information for adult female common dolphins (Perrin et al. 1985; Heyning and Perrin 1991) with lengths of "adult females."

Data Source	Neritic or Long-Beaked	Northern	Central	Southern
Specimen Data				
mean	207.7	178.5	194.3	188.5
range	193-224	155-200	170-215	180-198
n	10	82	306	6
Photographic Data				
mean	206.2	179.2	194.8	184.3
range	185-217	159-200	169-212	172-197
n	5	100	41	20

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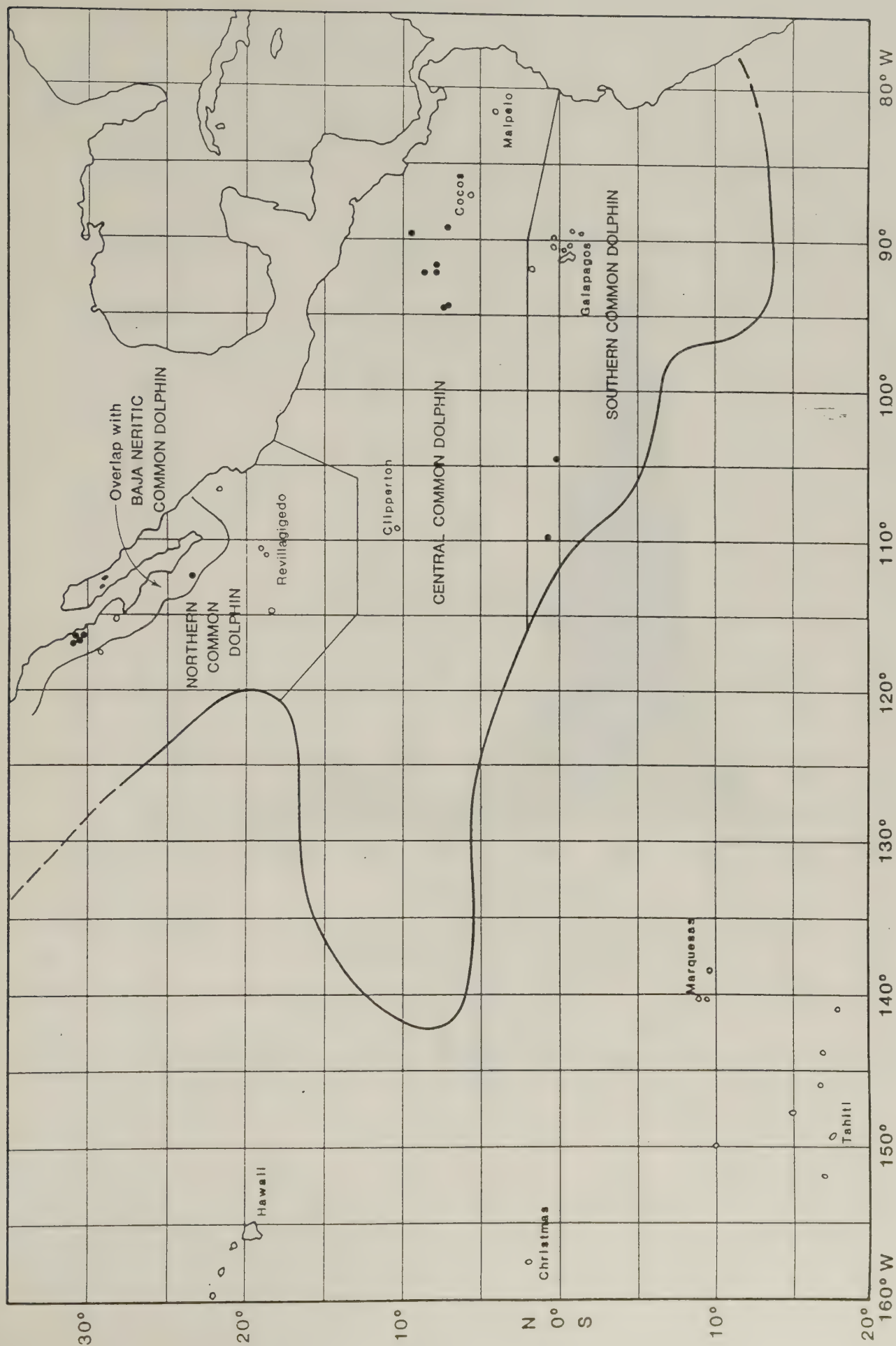


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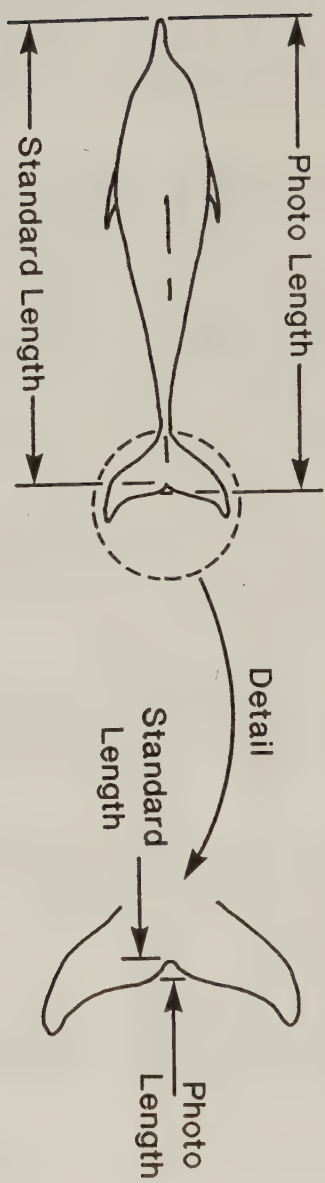


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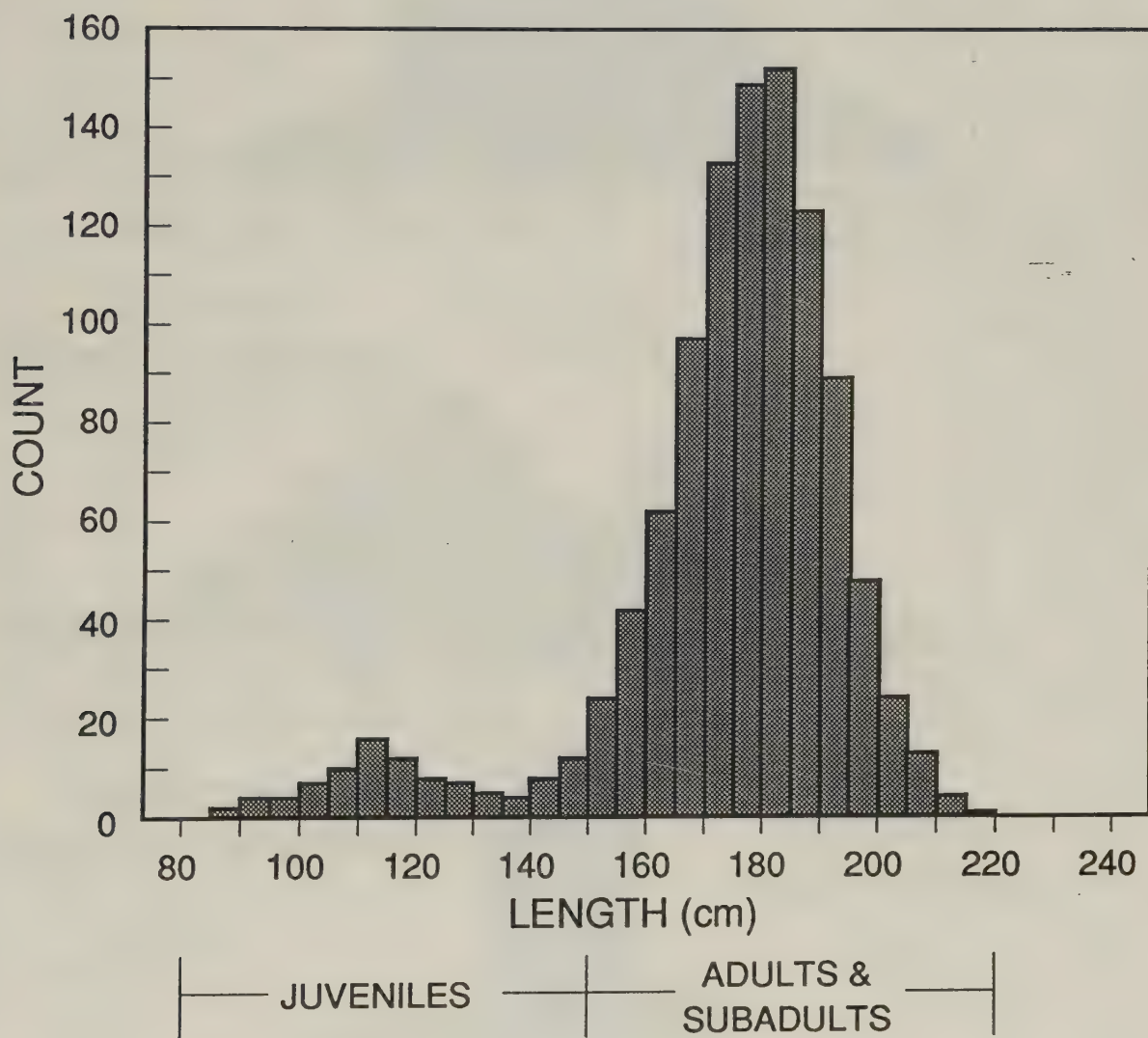


Fig. 3. Histogram of lengths for common dolphins from the northern region.

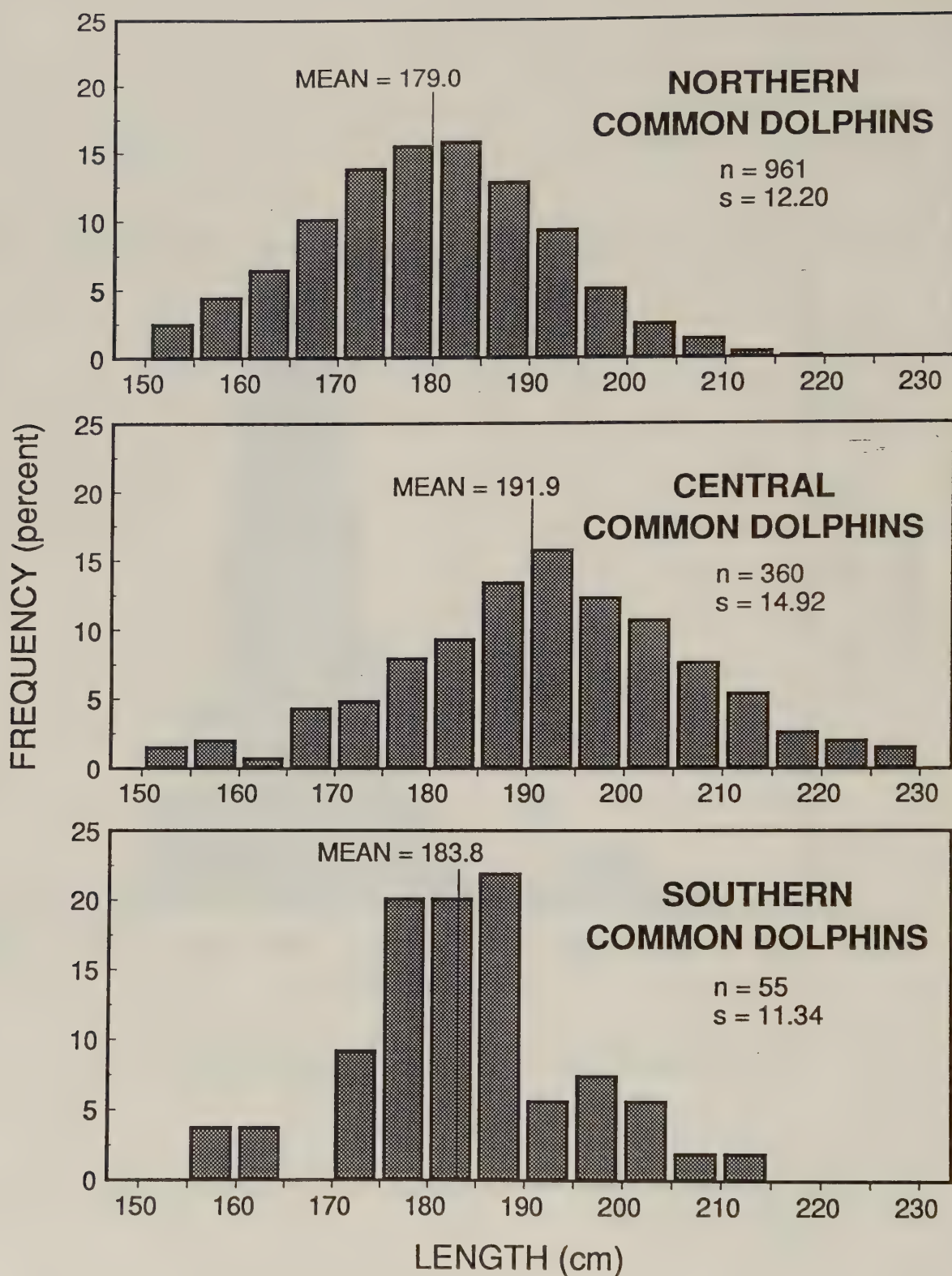


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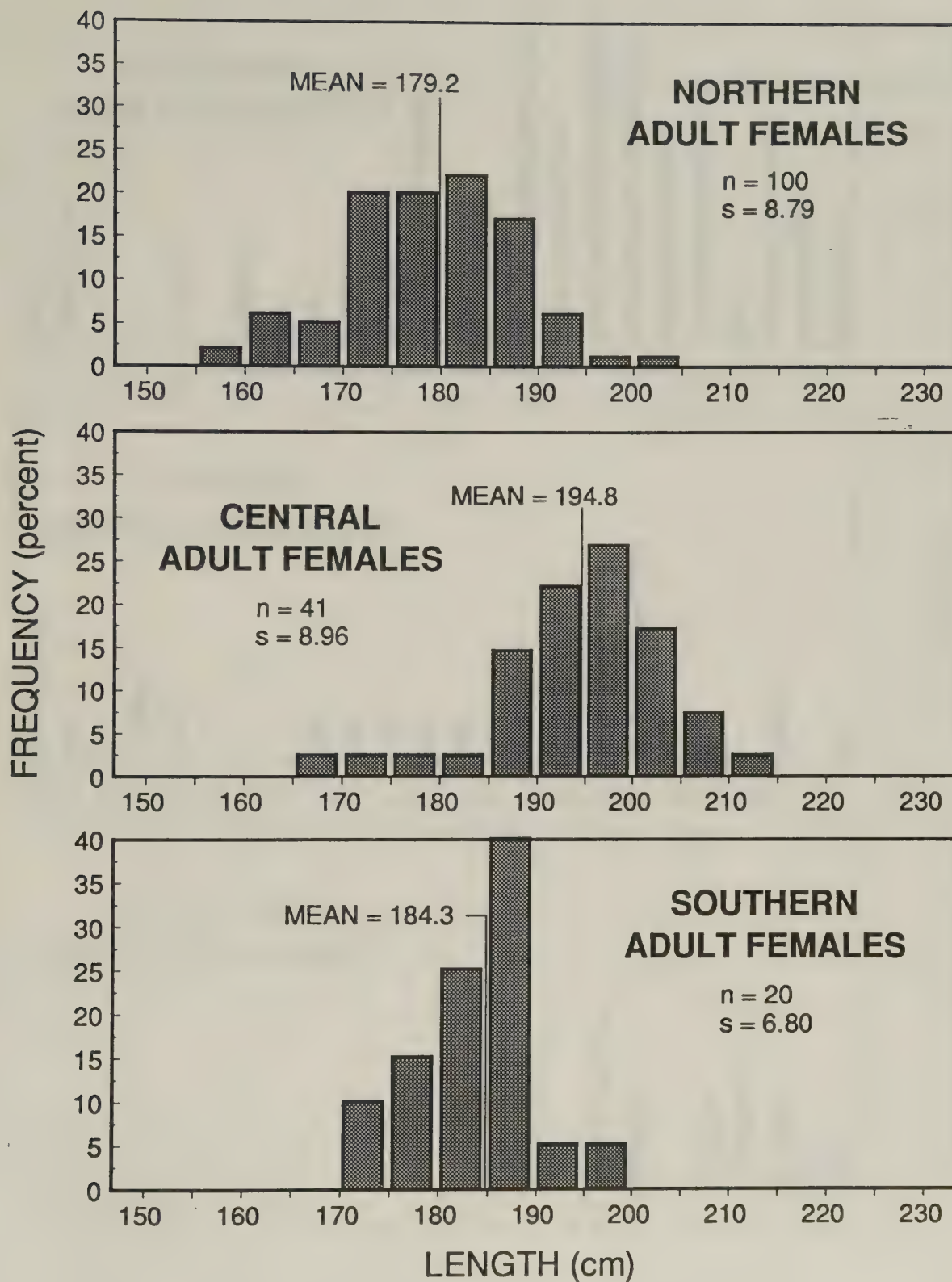


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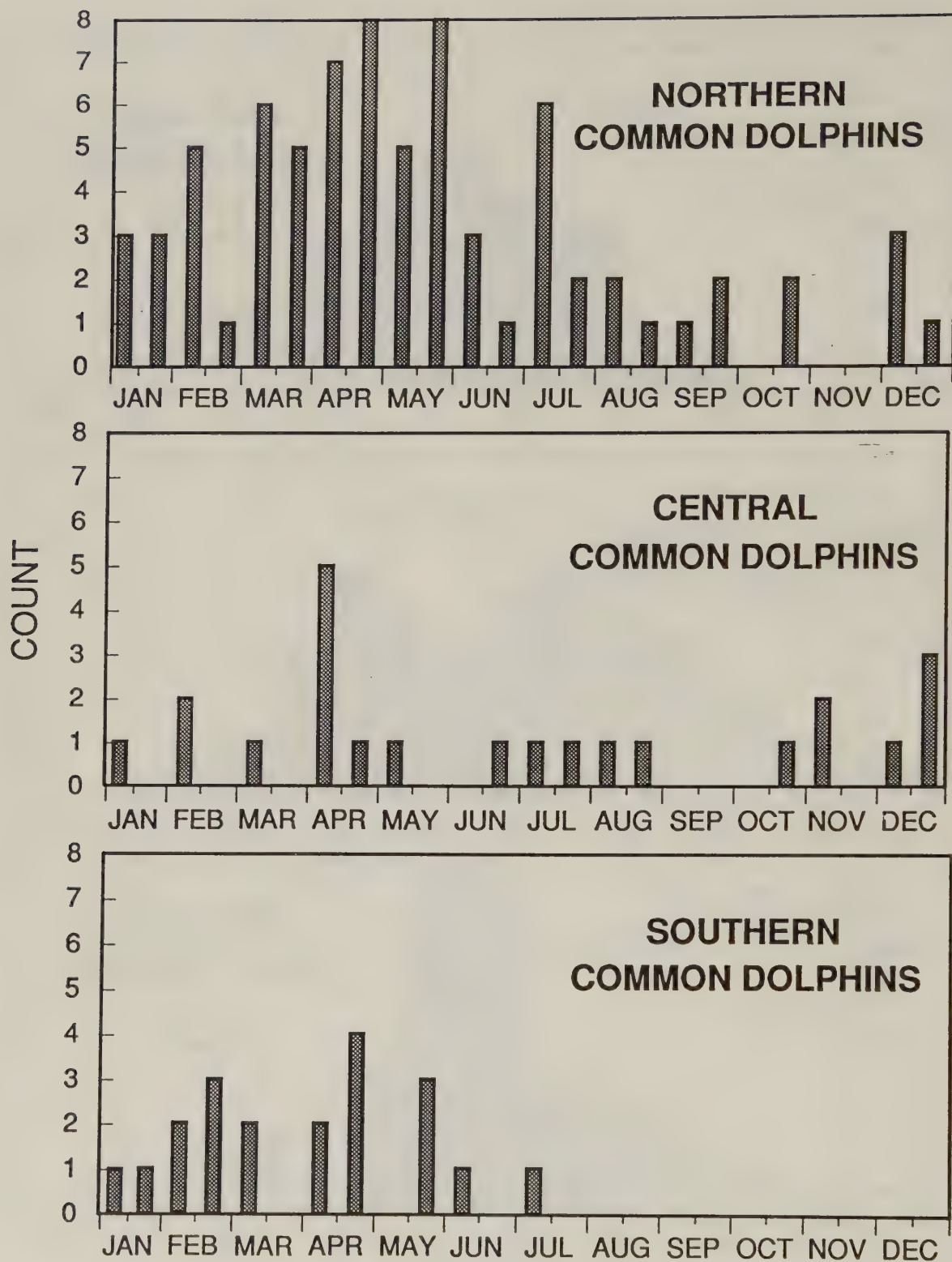


Fig. 6. Distribution of calculated birth dates for common dolphins from three geographic areas.

Northern Common Dolphin - Cumulative Birth Date Distribution

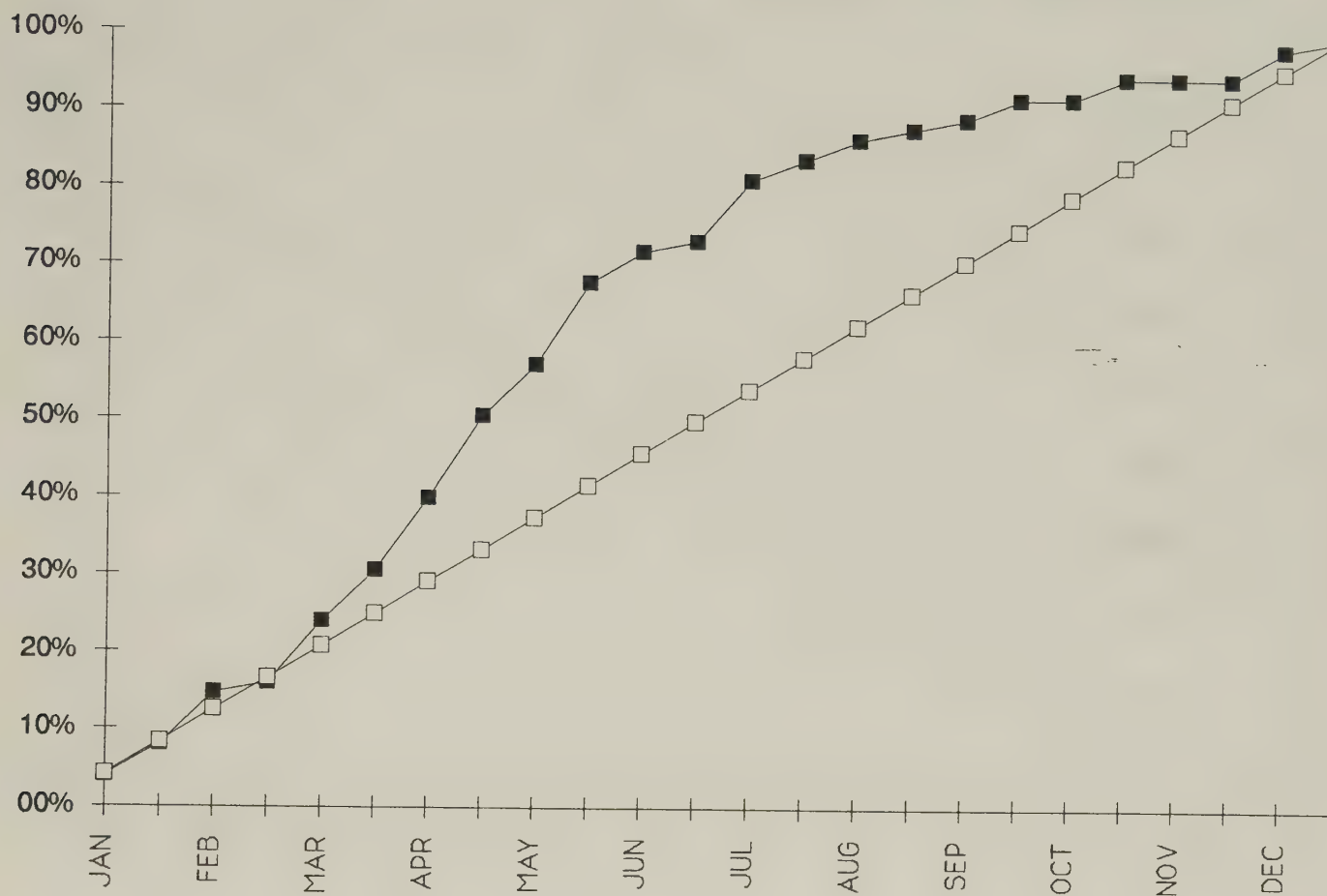


Fig. 7. Cumulative distribution of calculated birth dates for common dolphins from the northern region. Plot of open boxes indicates cumulative distribution if births were uniform throughout the year.

Central Common Dolphin - Cumulative Birth Date Distribution

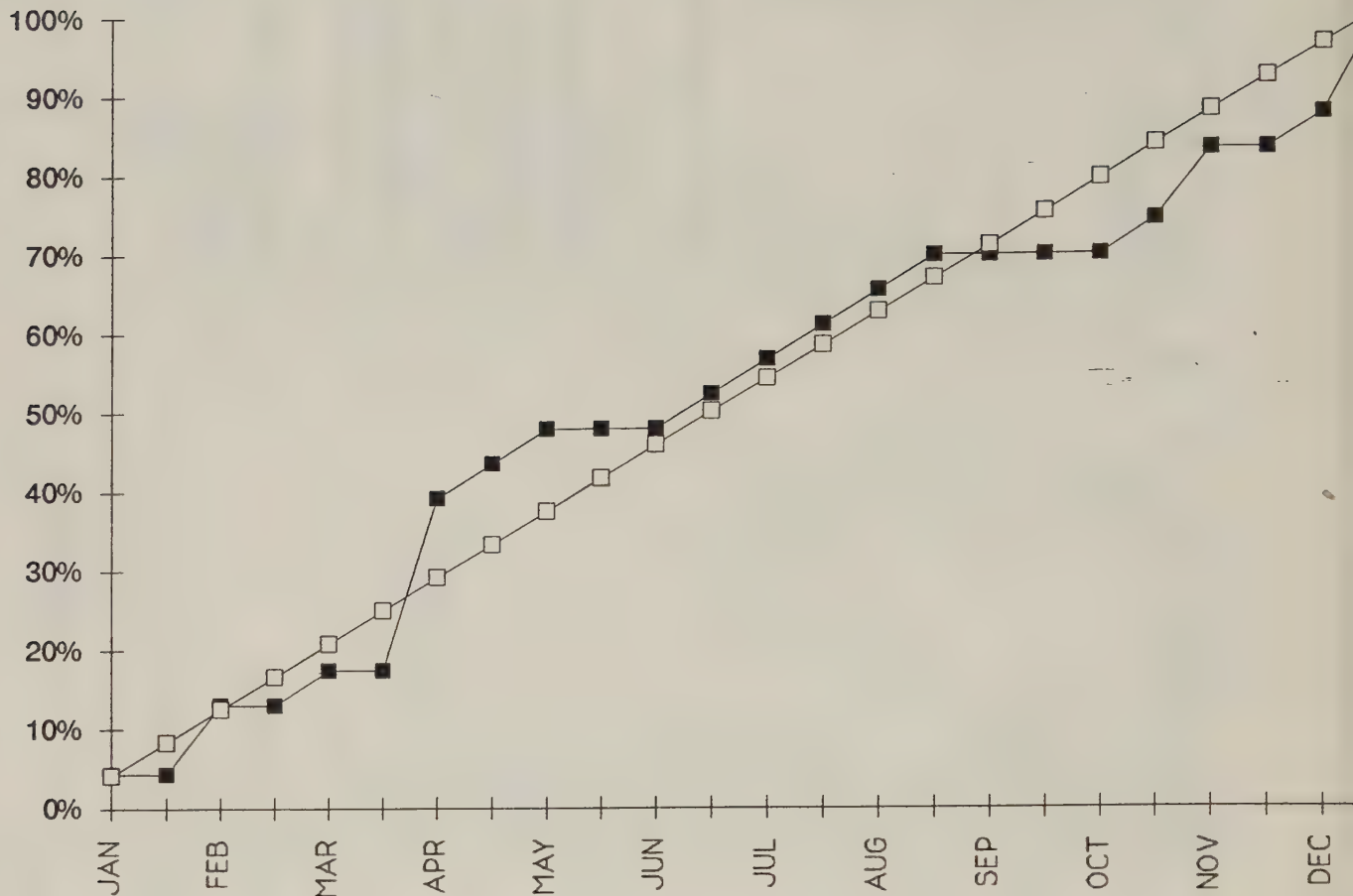


Fig. 8. Cumulative distribution of calculated birth dates for common dolphins from the central region. Plot of open boxes indicates cumulative distribution if births were uniform throughout the year.

Southern Common Dolphin - Cumulative Birth Date Distribution

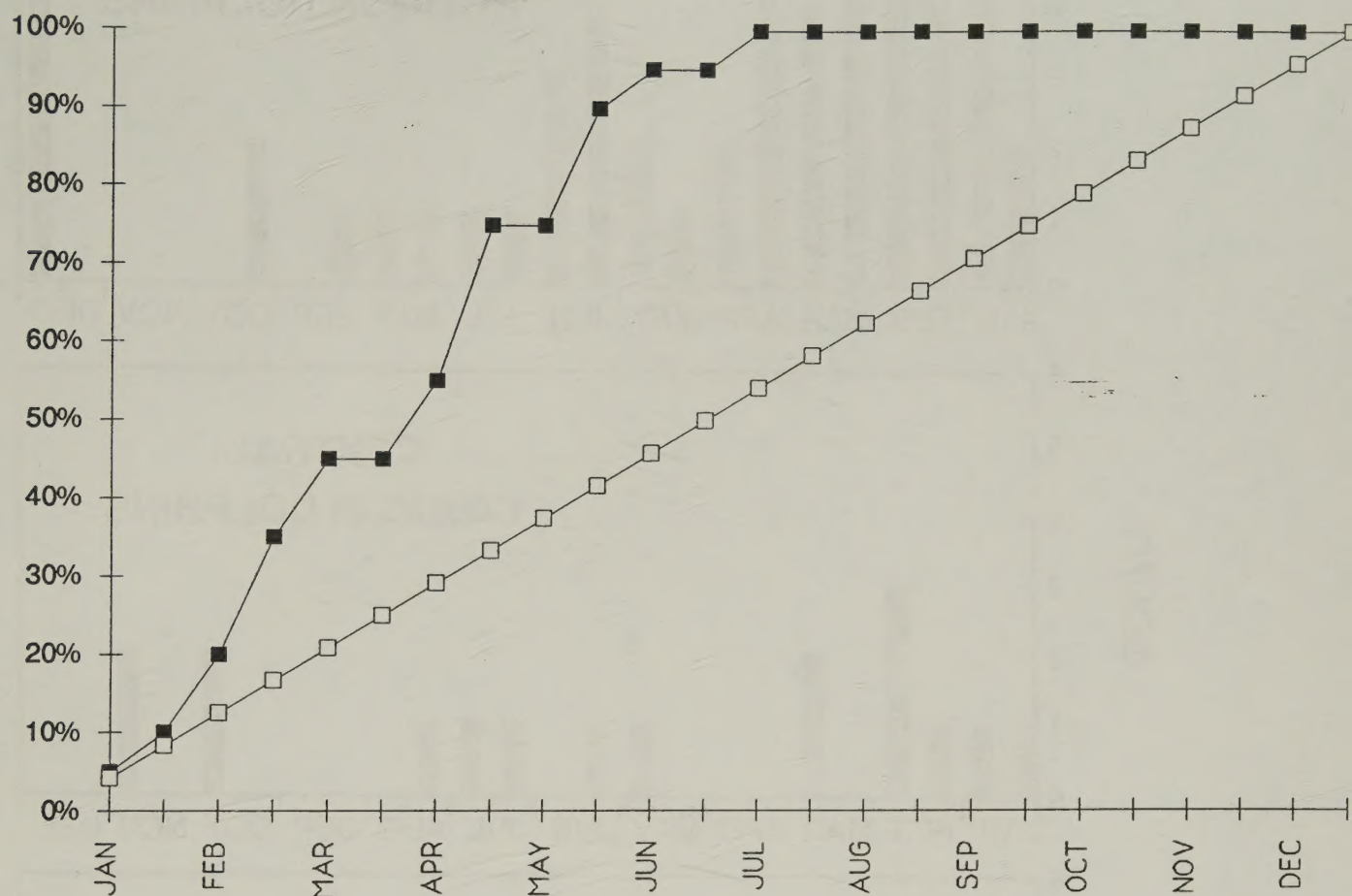


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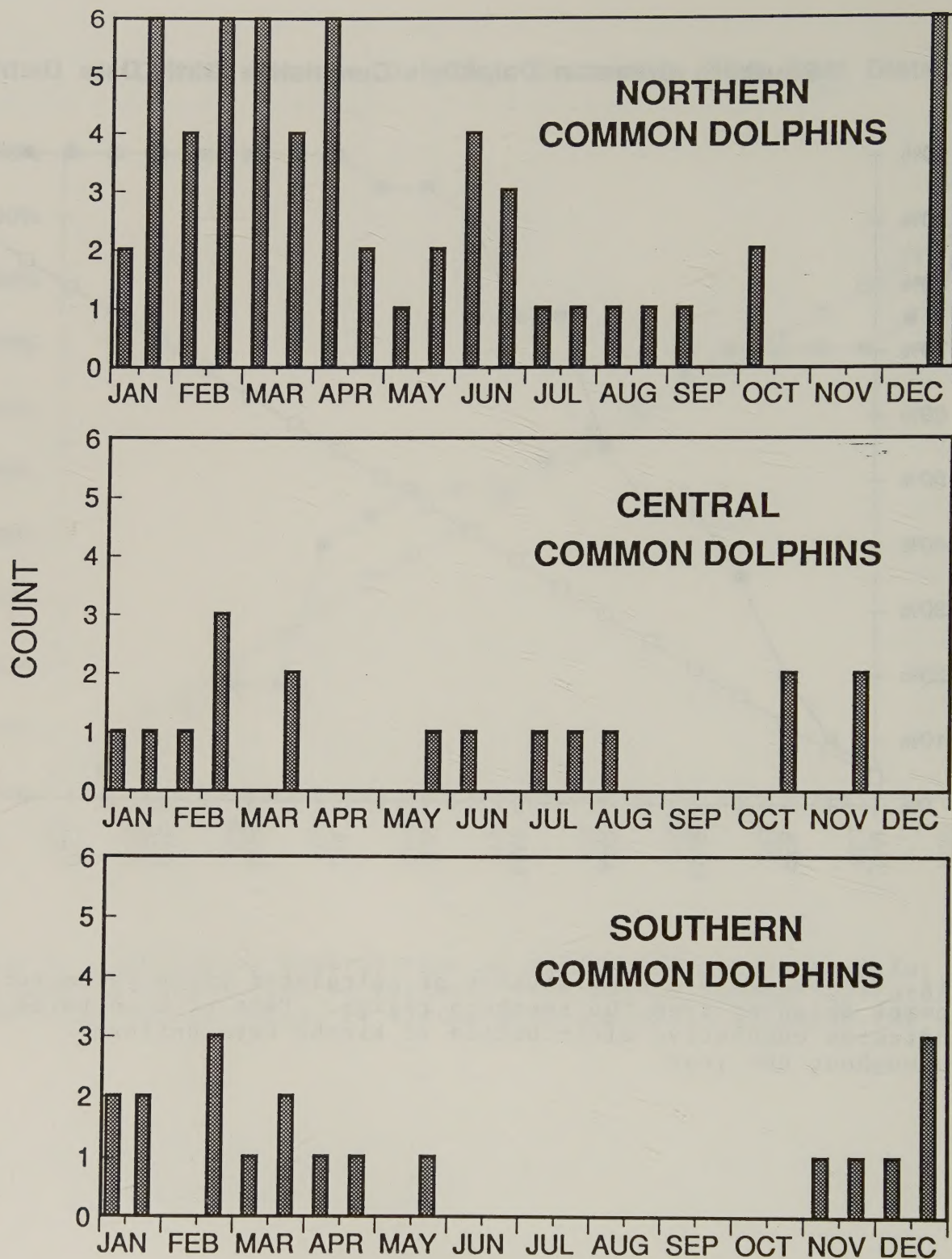


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